LIFE HISTORY AND DESCRIPTIONS OF IMMATURE STAGES OF TEPHRITIS BACCHARIS (COQUILLETT) ON BACCHARIS SALICIFOLIA (RUIZ & PAVON) PERSOON IN SOUTHERN CALIFORNIA (DIPTERA: TEPHRITIDAE)

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Abstract. – Tephritis baccharis (Coquillett) is bivoltine and monophagous on Baccharis salicifolia (Ruiz & Pavon) Persoon in southern California. The egg, second and third instar larvae, and puparium are described and illustrated. Eggs are inserted singly into terminal buds of main and axillary branches in late winter or early spring. First instar larvae hatch and tunnel into the pith just basad to the apical bud where they initiate gall formation. Gall and larval growth continue slowly into the fall, when pupation occurs. Most F_1 flies emerge, mate, and after about one week begin oviposition. Some F_1 flies that emerge in the fall may overwinter as adults; however, a few F_1 individuals may not emerge and instead overwinter as pupae in puparia in mature galls. Second and third instar, F_2 larvae also overwinter in developing galls. Flies were long-lived under laboratory conditions; males and females lived an average of 140 days and 83 days, respectively. This longevity and the long fecundity period of females allow *T. baccharis* to attack the new buds and branch growth produced by *B. salicifolia*, because this phraetophyte is capable of protracted, nearly year-round vegetative growth and flowering in southern California.

Principal natural enemies of *T. baccharis* include three, solitary, primary, parasitoids, *Pnigalo* sp. (Hymenoptera: Eulophidae), *Halticoptera* sp. and *Pteromalus* sp. (Hymenoptera: Pteromalidae), and unidentified birds as important predators on overwintering larvae in galls.

Key Words. - Insecta, biology, gall, parasitoids, bird predation, mating behavior, chemosensilla

Among 18 described species of *Tephritis* indigenous to North America (Foote 1960, Stolzfus 1977, Foote & Blanc 1979, Jenkins & Turner 1989), only the biology of *T. stigmatica* (Coquillett) on *Senecio* spp. heretofore was well known (Tauber & Toschi 1965, Goeden 1988a). This paper details the biology of a second Nearctic species, *T. baccharis* (Coquillett), on *Baccharis salicifolia* (Ruiz & Pavon) Persoon [= *B. glutinosa* Persoon and *B. viminea* deCandolle (McVaugh 1984)], Asteraceae in southern California.

Interest has been expressed in the biological control of *B. salicifolia* (Boldt & Robbins 1990), other *Baccharis* spp. (Boldt & Robbins 1987, Boldt et al. 1988), and other indigenous weeds (Pemberton 1985) in the U.S. with natural enemies obtained from South America. Also, stenophagous *Baccharis*, feeding insects from North America have been imported to Australia for the biological control of *B. halimifolia* L. (Palmer 1987, Julien 1987, Palmer & Bennett 1989).

MATERIALS AND METHODS

Field observations, laboratory examination, and the rearing of field collected galls from several locations (see below) in southern California during 1983–1990 provided most of the information reported herein. These field data were supplemented by laboratory cagings, in 1989, of single males and females or paired reared adults of opposite sex. The adults were reared in 850 ml, clear plastic cages

fitted with screened lids for ventilation and basal water reservoirs in which absorbant cotton wicks and bouquets of excised vegetative branches of *B. salicifolia* were emersed through a hole in each cage bottom. Honey striped with a bulb and syringe on the underside of the lids provided food for the flies. Flies or parasitoids were reared from larvae and puparia dissected from galls held separately in cottonstoppered, glass, shell vials within humidity chambers at 22–24° C and 76% RH.

Plant names follow Munz (1974) and McVaugh (1984); tephritid names follow Jenkins & Turner (1989). Voucher specimens of T. baccharis from each study site are located in the research collection of RDG (Department of Entomology, University of California, Riverside). RDG also has established a separate collection of hymenopterous parasitoids of California Tephritidae; DHH has established a separate collection of immature Tephritidae.

Immature stages were described from two eggs dissected from buds (laboratory cagings), a second and third instar larva, and a puparium dissected from galls. Larvae and eggs were treated for scanning electron microscopy (SEM) as described in Headrick & Goeden (1990a). Specimens were examined and micrographs prepared at 15 kV accelerating voltage, using Polaroid SS P/N film on a JEOL JSM-C35 SEM, located in the Department of Nematology, University of California, Riverside. The third instar larva is described in detail using the nomenclature and format adopted by Headrick & Goeden (1990a); the second instar larva description is limited to observed differences. Means \pm SE are provided throughout the paper.

TAXONOMY

Coquillett (1894) described *T. baccharis* as a *Trypeta*. Jenkins & Turner (1989) revised the *Baccharis*-infesting tephritids of North America, reviewed the taxonomy, designated the lectotype, illustrated and measured ova, and described and illustrated important characters of adult *T. baccharis*.

Egg. – Five eggs dissected from oviposition punctures (Fig. 1A) were white, fusiform, 0.68 \pm 0.02 mm long and 0.26 \pm 0.01 mm wide. The chorion is reticulated and the apex bears a 0.04 mm button-like, honey-combed pedicel (Fig. 2A). Polygonal reticulation of the chorion (Fig. 2B) is common to all eggs of Tephritidae examined to date (by DHH), but is highly developed in *Tephritis* species, especially *T. baccharis* (Jenkins & Turner 1989). An unusual feature of the reticulation is its differential complexity. The end embedded in plant tissue has more shallow fenestrations (Fig. 2C), which increase in height and become topped with papillae toward the heavily ridged pedicel (Fig. 2D). The plant itself may provide some measure of protection for the smooth end of the egg, which probably has little gas exchange function for the developing embryo, because it is inside plant tissue. The polygonal reticulation strengthens the exposed chorion, protecting not only the embryo, but also the pedicel through which most gas exchange probably takes place (as seen in a more exaggerated form in the eggs of *Paracantha gentilis* Hering [Headrick & Goeden 1990a]).

Third Instar Larva. – A single third instar larva measured 5.3 mm long and 2.5 mm wide (Fig. 3A). It is creamy white, superficially smooth, elongate, cylindrical, tapered and bluntly rounded anteriorly, and gradually increasing in width to its truncate posterior end.

The gnathocephalon is less conical and more reduced, and the rugose pads are

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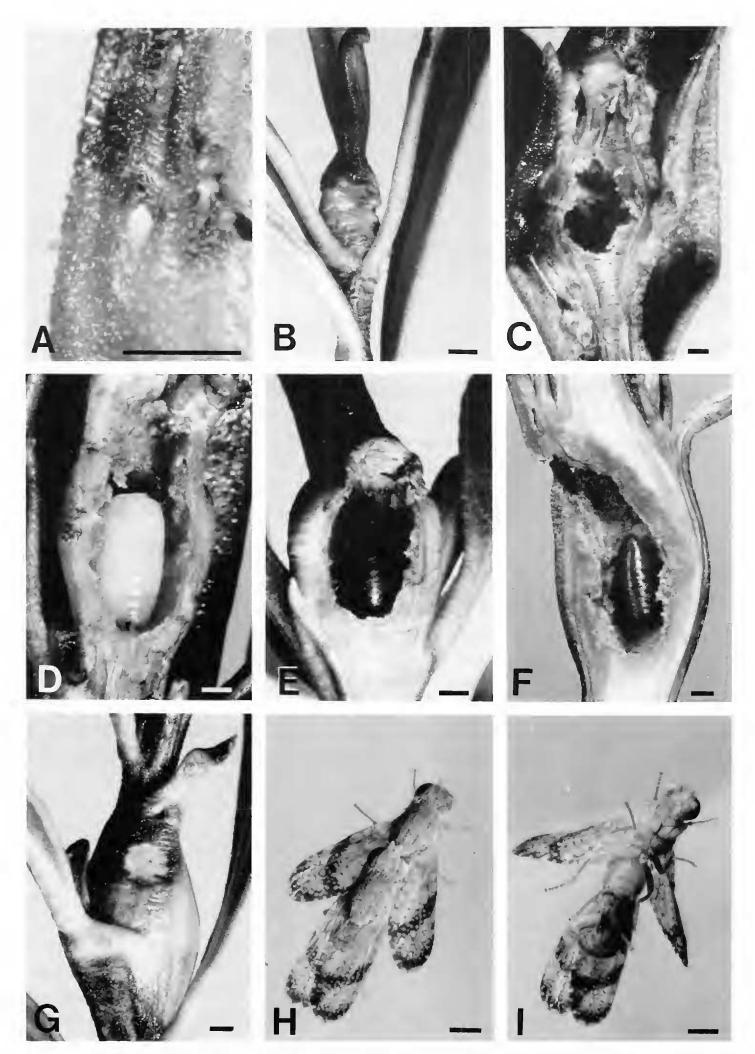


Figure 1. Life stages and galls of *Tephritis baccharis* on *Baccharis salicifolia*: (Bar = 1 mm) (A) egg protruding from ovipositional puncture in bud; (B) lateral view of small, immature gall; (C) sagittal section through small immature gall exposing feeding chamber; (D) third instar larva in feeding chamber in full-size gall; (E) gall with apical meristem killed by larval feeding; (F) puparium in feeding chamber below exit tunnel for adult; (G) lateral view of mature gall with round window through which adult emerges; (H) mating adults, dorsal view; (I) mating adults, ventral view.

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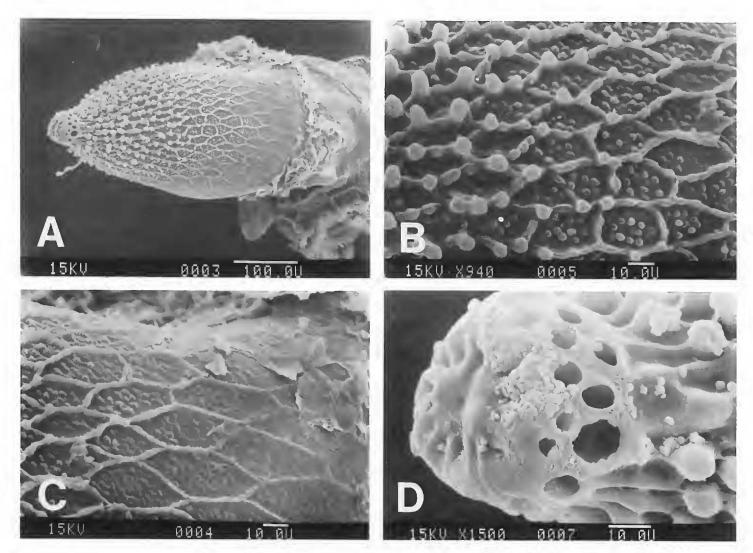
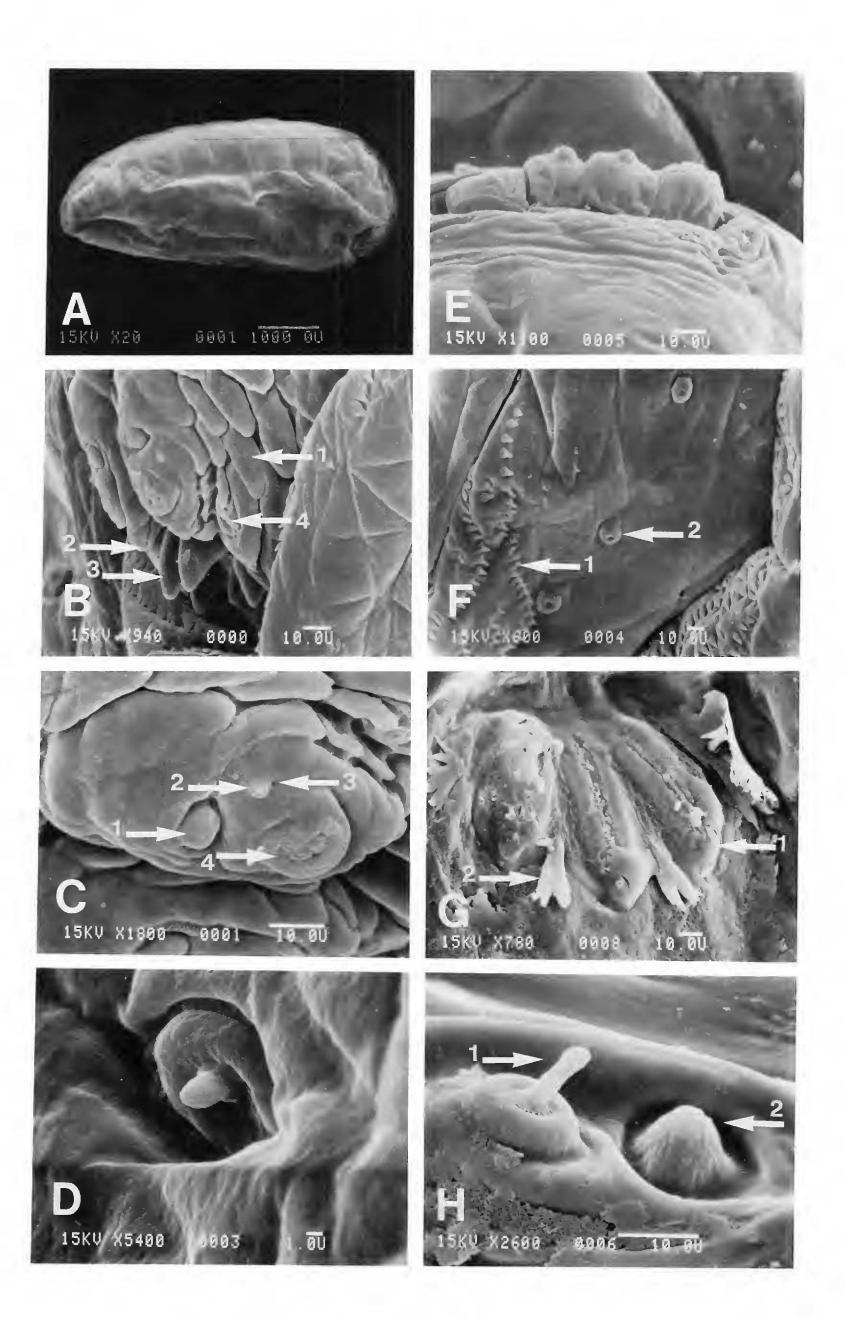


Figure 2. Egg of *T. baccharis*: (A) habitus, dissected from *B. salicifolia*; (B) detail of polygonal reticulation; (C) detail of point of insertion into plant tissue; (D) pedicel at exposed end of egg.

more dorsoventrally elongate than in most species of tephritid larvae examined by us to date (Fig. 3B: 1). The gnathocephalon bears flattened anterior sensory lobes separated by a medial depression (Fig. 3C). The paired dorsal sensory organs lie just dorsad of the anterior sensory lobes and are composed of a single papilla (Fig. 3C: 1). The sensory lobes bear the lateral sensory organ, the pit sensory organ and the terminal sensory organ (Fig. 3C: 2, 3, 4), which share the same structure and placement as with other tephritid larvae examined to date (DHH, unpublished data). The integumental petals which surround the mouth lumen (Fig. 3B: 2) are much reduced in comparison with other tephritid larvae (e.g., Stenopa affinis Quisenberry [Goeden & Headrick 1990]). The mouth hooks are heavily sclerotized and tridentate. The teeth are stout and bluntly conical (Fig. 3B: 3). A median oral lobe, which was not visible with SEM, was observed with a dissecting microscope; this brings the total number of nonfrugivorous tephritid larvae with a median oral lobe to 15 species (Headrick & Goeden 1990a; Goeden & Headrick 1990; DHH, unpublished data). Lateral lobes bearing several sensilla were located dorsolaterally on the edge of the mouth lumen (Fig. 3B: 4), are similar in placement, and share similar types of sensilla to those observed in S. affinis (Goeden & Headrick 1990).

The prothorax is smooth and bears several flattened sensilla. Larvae of Tephritidae typically have flattened sensilla on the prothorax (Foote 1967, Headrick & Goeden 1990a); however, *T. baccharis* has at least four sensilla, each with a finger-like projection surrounded by a collar. These sensilla may be mechanically



stimulated by deflection (Fig. 3D). The anterior thoracic spiracle is located dorsolaterad on the posterior margin and bears four papillae, each in turn topped with a distinct, smooth, rounded smaller papilla (Fig. 3E).

The succeeding segments are superficially smooth and demarcated by a depression that circumscribes the body. The integument adjacent to the segmental line is reticulated with shallow depressions and has intersegmental bands of minute acanthae (Fig. 3F: 1). Each segment bears a group of three sensilla arranged in a vertical row, posterior to the segmental line on the lateral aspect of the body (Fig. 3F: 2). The sensilla are smooth with a central pore, and are similar in shape and placement to the lateral sensilla described for *S. affinis* (Goeden & Headrick 1990).

The caudal segment bears the posterior spiracular plates composed of three elongate oval rimae about 0.07 mm long (Fig. 3G: 1), and four interspiracular processes with two to five branches; the longest process measured 0.03 mm in length (Fig. 3G: 2). The caudal segment also has the typical arrangement of sensory papillae that includes dorsal, lateral and ventral pairs of finger-like projections in a basal collar located on the posterior margin of the body (Fig. 3H: 1). A tuberculate chemosensillum is associated with each of the two dorsal sensilla in a shallow depression (Fig. 3H: 2). On the apex of the chemosensillum is a raised crown that bears several open pores. This sensillum has not been observed or described for any other tephritid larva to date (DHH, unpubl. data).

Second Instar Larva. —A second instar larva dissected and examined from an overwintering gall measured approximately 3.5 mm long and 1.5 mm wide (Fig. 4A). It is a translucent white, cylindrical, with a cone-shaped gnathocephalon, and rounded posteriorly. Most structures were similar in shape and placement to those of the third instar larva. The gnathocephalon is slightly rugose, with elongate pads as seen in the third instar. The anterior lobe is flattened and bears all three sensory organs as well as the closely associated dorsal sensory organ. The mouth hooks are bidentate and not bluntly rounded at the apex as in the third instar larva. The posterior spiracular plates bear three rimae and interspiracular processes with one or two blades about 0.01 mm in length.

Puparium. – Fifty-two of 61 puparia of T. baccharis dissected from galls averaged 1.99 ± 0.03 (range, 1.50-2.31) mm in widest width, and 40 of these that were intact averaged 4.37 ± 0.07 (range, 3.34-5.59) mm in length. The puparia are superficially smooth, distinctly segmented, elongate ellipsoidal, anteriorly rounded, and slightly flattened posteriorly and dorsoventrally. The anterior end bears the invagination scar of the mouth and the anterior thoracic spiracles (Fig. 4B: 1, 2). The posterior end is finely wrinkled without protruding spiracular plates (Fig. 4C). One of 61 puparia dissected from galls was mostly unpigmented and black only at both ends; all other puparia were uniformly black. Goeden (1988a)

Figure 3. Third instar larva of *T. baccharis*: (A) habitus, anterior end at left; (B) detail of gnathocephalon, 1-rugose pads, 2-integumental petals, 3-mouth hooks, 4-lateral sensory lobes; (C) anterior sensory lobes (dorsal at left), 1-dorsal sensory organ, 2-lateral sensory organ, 3-pit sensory organ, 4-terminal sensory organ; (D) sensillum on anterior of prothorax; (E) anterior thoracic spiracles; (F) lateral aspect of the body, 1-acanthae, 2-lateral sensilla; (G) posterior spiracular plate (dorsal at right), 1-rimae, 2-interspiracular processes; (H) posterior sensilla, 1-finger-like process, 2dome sensillum.

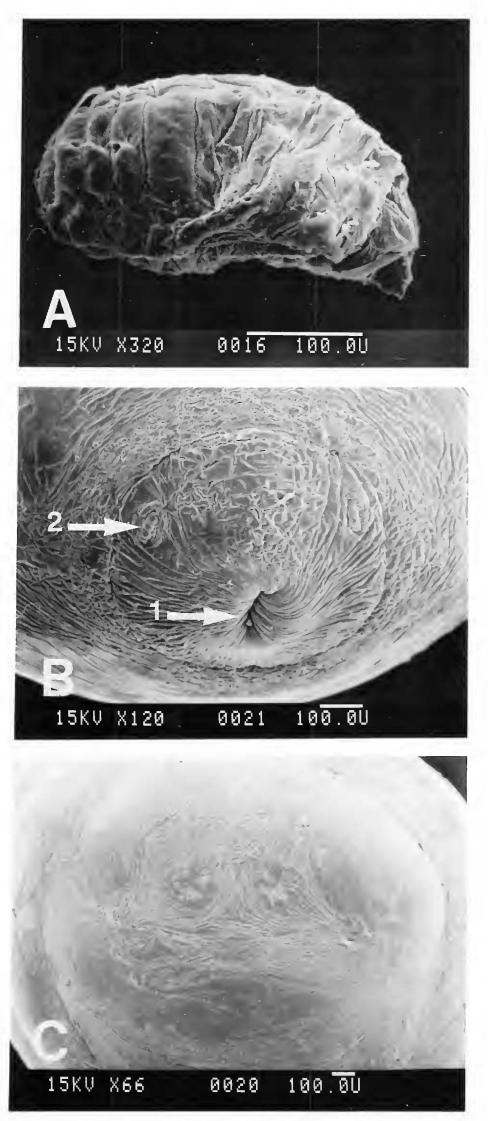


Figure 4. Second instar larva and puparium of T. baccharis: (A) habitus, second instar (anterior at right); (B) anterior end of puparium, 1—mouth invagination, 2—anterior thoracic spiracles; (C) posterior end of puparium.

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reported incomplete pigmentation of some *T. stigmatica* puparia. This color variation also has been observed among some flower head infesting *Trupanea* (Goeden 1988b), gallicolous *Procecidochares* spp. (RDG, unpublished data), and was reported by Headrick & Goeden (1990a) among puparia of *Paracantha gentilis* Hering.

DISTRIBUTION, HOST, AND STUDY SITES

Jenkins & Turner (1989) described the range of T. baccharis as "eastcentral Mexico northwest to westcentral California." The distribution of its only known host plant, *B. salicifolia* (Wasbauer 1972, Jenkins & Turner 1989) was described by Boldt & Robbins (1990) as "common along waterways in the southwestern United States and northern Mexico as well as western and southern South America."

Tephritis baccharis has been reared only from bud galls on *B. salicifolia*, never from capitula of this or any other species of *Baccharis* or Asteraceae widely sampled throughout California since 1980 (RDG, unpublished data). Nearctic species of *Tephritis* are either obligate or facultative gall formers on branches or stems, or ovule feeders in capitula (Foote 1960; Tauber & Toschi 1965; Jenkins & Turner 1989; Goeden 1988a; RDG, unpublished data). *Tephritis baccharis* is a monophagous, obligate gall former.

Our field study locations for flies and galls augment the California and southwestern U.S. distributions plotted by Foote & Blanc (1963) and Jenkins & Turner (1989), respectively: W end of Central Valley, Laguna Canyon, and Cebada Canyons (Goeden 1983), Santa Cruz Island, Santa Barbara Co., 8–13 Oct 1983; Big Morongo Canyon, Riverside Co., 7 Mar 1985, 3 Apr 1986, 23 Jan 1989, 30 Jan 1990; Oriflamme Canyon, NW San Diego Co., 8 Mar 1989. Additional locations where the characteristic galls on *B. salicifolia* were observed or collected included: Canebrake Creek, N of Spring Canyon, NW Kern Co., 3 Mar 1987; Mission Canyon, Riverside Co., 2 Apr 1987; Scissors Crossing, NW San Diego Co., 19 Dec 1989 and 9 Jan 1990. This fly, like *B. salicifolia*, is widely distributed in riparian habitats in southern California; however, its galls were not observed at many other locations where flower heads of this dioecious shrub sampled yielded other Tephritidae (Goeden 1983; RDG, unpublished data).

Biology

Egg. – In laboratory cagings, eggs were inserted for all or most of their lengths, mainly into apical buds, and a few into axillary buds. Only the highly reticulated, pedicellar ends slightly projected beyond or below the edges of the longitudinal egg punctures (Fig. 1A). Three egg punctures measured 0.55 mm long by 0.15 mm wide. The long axes of the egg bodies, buds, and branches were parallel. Bud tissues turned necrotic in areas immediately surrounding the eggs, as reported for *Eutreta diana* (Osten Sacken), another gallicolous tephritid (Goeden 1990). One unhatched egg contained an embryo with its partly pigmented cephalopharyngeal skeleton located at the pedicellar end; however, the first instar larva always ecloses through a slit in the chorion near the end opposite the pedicel, and immediately begins tunneling basipetally. Apparently the embryo of *T. baccharis* turns 180° just before eclosion, like several other species of nonfrugivorous Tephritidae (Varley 1937, Cavender & Goeden 1982, Goeden 1987, Goeden et al. 1987). This

behavior apparently evolved to allow instant entry by the delicate, newly eclosed first instar larvae into moist, host plant tissues, and also to accommodate embryo respiration via the exposed pedicel (Headrick & Goeden 1990a).

All galls examined contained only one larva or puparium, indicative of only one egg having been oviposited in each bud in nature; however, in cagings, where ovipositional sites were scarce, as many as 10 eggs were inserted in a single apical bud. Similarly, in the field, most current generation galls were solitary at ends of separate branches; only one branch from Oriflamme Canyon bore two similar aged galls connected by a narrow neck of ungalled internode. Both sexes of *B. salicifolia* bore galls of *T. baccharis*.

Larva. – Two newly hatched larvae averaged 0.49 mm in length. The first instar tunneled until it reached the pith of the branch just basad to the apical meristem. The necrotic tunnel of one first instar was traced for 9 mm from this incipient gall site distally to its empty egg chorion. The young larva settles, molts, and initially excavates a small ellipsoidal cell about 3 mm long and <2 mm wide in the juvenile gall, evidenced externally as only a slight swelling of a branch terminal (Figs. 1B, 1C). Here, it feeds and develops (perhaps sporadically) through the summer or the following fall and winter, depending upon which generation it represents, F_1 or F_2 , respectively (see below). The molt to the second instar could be ascertained by the presence of a small, intact, cephalopharyngeal skeleton discarded at one end of the cell. Once plant growth begins in mid-winter to early spring, or is triggered once again later in the year by late summer rainfall as sometimes occurs in southern California, gall and larval growth are accelerated and proceed concurrently.

Twenty (87%) of 23 fully formed F_2 galls of the previous year's overwintering generation sampled at Oriflamme Canyon were fusiform; the remaining galls, subovoidal. The former shape resulted from continued growth of the bud at each gall apex; whereas, the latter shape resulted from death of the terminal bud from larval feeding by T. baccharis. Such intragenerational differences in shape also were noted among galls of T. stigmata by Goeden (1988a), and the causes for this difference were discussed relative to galls of E. diana by Goeden (1990). The galls of T. baccharis, like those of T. stigmatica, are shortened, thickened, succulent terminal parts of main or axillary branches (Figs. 1D, 1E). The 23 mature galls incorporated an average of 3.8 ± 0.3 (range, 1–6) nodes, and were smooth surfaced, light green and longitudinally striped or unilaterally colored red-purple when occupied. When empty, the galls turned tan, shriveled, and dehisced, or became woody and persisted as branch swellings. Externally, the 23 galls averaged 13.1 \pm 0.5 (range, 8–19) mm in length, and 5.6 \pm 0.2 (range, 4–7) mm in width. The larva feeds on the expanded pith parenchyma which comprises the bulk of the gall (Figs. 1C, 1D). The feeding larva eventually hollowed out an ellipsoidal, central, longitudinal, basally rounded cavity. This open feeding cavity was irregularly surfaced with yellow-white callose tissue, and averaged 5.5 \pm 0.2 (range, 4.4–7.8) mm in length and 2.7 \pm 0.1 (n = 23; range, 2.1–3.5) mm in width (Fig. 1D).

Twenty (66%) of 30, F_1 galls collected on Santa Cruz Island were fusiform; the remainder, subovoidal. These 30 galls incorporated 3.8 ± 0.1 (range, 3–5) axils and externally measured 20.4 ± 1.0 (range, 12–33) mm long by 8.3 ± 0.3 (range, 6–13) mm wide.

When fully grown, the larva extends the feeding cavity into an exit tunnel 1.7 \pm 0.1 (n = 23; range, 0.8–3.2) mm long, which may end apically (and thus kill the terminal bud, Fig. 1E), or more commonly ends subapically (Fig. 1F) in an oval to round, thin, cuticular window 1.6 \pm 0.1 (range, 1.1–2.1) mm in diameter (Fig. 1G).

Puparium. – Pupation occurs in the feeding chamber with the posterior end of the puparium resting on, or up to, about 1 mm above the bottom of the feeding chamber. The anterior end of the puparium normally faces the window to allow egress of the emerging adult (Fig. 1F).

Adult. – Five males and five females (F_1) emerged between 13 Nov and 6 Dec 1985 from galls collected on Santa Cruz Island during the previous October. Six males and three females emerged from 22 Mar to 5 Apr (overwintered F_2) from galls collected in Oriflamme Canyon in Mar 1989. Both sexes emerged throughout the emergence periods. Also, two females emerged from F_1 galls collected at Big Morongo Canyon on 23 Jan 1985. One male and one female emerged on 15 Jan 1990 from F_1 galls apparently containing these individuals as fully developed pupae within puparia collected at Scissors Crossing on 9 Jan 1990. These latter two rearing records demonstrate that some F_1 individuals also overwinter as puparia in galls.

Apparently females are polygamous, males are polyandrous. Females began to mate in laboratory cagings (n = 3) 1 to 2 days after their emergence. Pairs mated repeatedly; one pair mated on at least 17 different days, and for the last time when the female was 121 days old. Another pair caged together at emergence mated on each of the first 7 consecutive days after they emerged. Mating by virginal males and females in laboratory cagings was protracted, involving little courtship behavior and no apparent postmating behavior. The male mounted the female after a short period of mutual recognition evidenced when the flies stood face-to-face and alternately, slowly waved their wings three to seven times. The anal edge of each wing was turned downward as each wing was brought forward until nearly perpendicular to the substrate in supination (Headrick & Goeden 1990b). The male then jumped over and atop the female or mounted her from one side, forcibly spread her wings, and rapidly initiated coitus. The mating posture (Figs. 1H, 1I) was much like that illustrated and described by Tauber & Toschi (1965) for T. stigmatica. The hind tarsi of the male rest on the substrate or move back and forth along the oviscape to help position the female's terminalia, his midtarsi grasp the middle of her abdomen laterally, and his foretarsi clasp her abdomen at its juncture with the thorax. The mouthparts of the male are positioned above her scutellum; the mouthparts of both flies pump rapidly during copulation (four to five pumps/sec). The wings are held parallel to the substrate. The wings of the female are spread at about 80° and centered over her abdomen; those of the male are overlapped atop his dorsum or are spread up to about 30° (Figs. 1H, 1I). Except for their mouthparts, both flies generally remain motionless during copulation, although the female may groom her head and mouthparts with her foretarsi, occasionally bring one wing forward, or even walk about while carrying the male with his hind tarsi on or off the substrate. Matings were observed throughout the daylight hours, and in one instance was extended over 2 days and nights under artificial lighting. To avoid mating, a nonreceptive female turned in tight circles, flew at the male, or turned and walked away. Males also mounted,

rode, but did not couple with nonreceptive females. For example, one male daily mounted and remained in a mating posture atop a nonreceptive female for up to 6 h on each of 4 consecutive days after they last mated, but without coupling with her.

Females began oviposition in bouquets in cages 1–2 weeks after emergence. Probing did not always result in oviposition. An average of about one egg per day was laid by each of seven females (range, 0.4-2 eggs daily). The oldest female was 65 to 72 days old when she last oviposited. Five males lived an average of 140 (range, 58–196) days; three females, 83 (range, 38–142) days. Tauber & Toschi (1965) reported the laboratory longevity of *T. stigmatica* adults when fed water, sugar, and enzymatic protein hydrolysate of yeast as 6 to 187+ days. Long-lived adults occur more widely among nonfrugivorous Tephritidae than is generally recognized (Christenson & Foote 1960, Freidberg 1984). Whether longevity among nonfrugivorous species correlates with the presence or absence of symbionts in the adult as suggested by Harris (1989) remains to be addressed experimentally.

Seasonal History. – Tephritis baccharis usually is bivoltine on B. salicifolia in southern California, but may be univoltine at some desert locations during dry years, as reported with Procecidochares sp. by Silverman & Goeden (1980). Tephritis baccharis does not additionally reproduce in capitula of the same host species or of an alternate host, as do T. stigmatica (Coquillett) (Tauber & Toschi 1965, Goeden 1988a), T. arizonaensis Quisenberry (Goeden 1983; Jenkins & Turner 1989; RDG, unpublished data), T. palmeri Jenkins, and T. subpura (Johnson) (Jenkins & Turner 1989). However, the combination of long-lived adults and long-fecund females in T. baccharis and a host phraetophyte capable of nearly year-round growth and flowering under southern California conditions (Munz 1974), can lead to localized overlapping and obscuring of fly generations. This reproductive flexibility on the part of T. baccharis facilitates utilization of buds and new branch growth on its host plant, which itself shows reproductive flexibility, traits useful for survival in drainages with high water tables and riparian habitats in otherwise harsh, arid environments.

Natural Enemies. — Three species of chalcidoid Hymenoptera were reared from T. baccharis during this study. Three females of Pteromalus sp. (Pteromalidae) were recovered from puparia as solitary endoparasitoids. Two males of Halticoptera sp. (Pteromalidae) were reared as solitary, larval ectoparasitoids. One female of Pnigalo sp. (Eulophidae) was recovered from a small gall as a solitary, ectoparasitoid of an early stage larva of T. baccharis.

Large holes in the sides of empty galls matched symptoms of predation by birds, probably bush tits, *Psaltriparus* sp., recently documented for galls of *Eutreta diana* (Goeden 1990). Five (14%) of 35 galls sampled from Oriflamme Canyon yielded parasitoids; five more galls suffered bird predation. Fifty-nine (69%) of 86, mainly F_2 galls of all sizes collected in Big Morongo Canyon on 30 Jan 1990 had been opened by birds and the larvae within removed.

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